THE CONTRIBUTION OF LEAF ARCHITECTURE AND WOOD ANATOMY TO CLASSIFICATION OF THE RHIZOPHORACEAE AND ANISOPHYLLEACEAE[1]

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ABSTRACT

Leaf-architectural and wood-anatomical data on the 18 genera traditionally considered to comprise the Rhizophoraceae were analyzed for insight on the intergeneric affinities. The four genera of the tribe Anisophylleae, considered on other lines of evidence to comprise the family Anisophylleaceae, are not readily separated using new data from leaf structure, or from a new look at the wood-anatomical literature. Leaves of both families are elliptic, and few features distinguish the two families or help separate the tribes of Rhizophoraceae s. str. or help separate the tribes. Anisophylleaceae have no marginal teeth or glands; they differ mainly from the Rhizophoraceae in having alternate leaves and no stipules. Leaves of the tribes Macarisieae, Gynotrocheae, and Rhizophoreae show some tribal-level variations in secondary venation, crystal type and distribution, and a few other features. The Rhizophoraceae leaves have an apiculate glandular tooth known as the Macarisioid type. Wood features, analyzed from the literature, do not readily distinguish the two families. Possible affinities of the Anisophylleaceae are not easily established using vegetative data. The Rhizophoraceae share a number of features with Celastraceae, Eleaocarpaceae, Hugoniaceae, Lepidobotryaceae, and Oxalidaceae.

The Rhizophoraceae are a family of tropical-forest and mangrove trees variously considered as comprising either 14 or 18 genera, a disparity coming from inclusion of the genera *Anisophyllea*, *Combretocarpus*, *Poga*, and *Polygonanthus* as a tribe Anisophylleae vs. their exclusion as the family Anisophylleaceae. Tobe & Raven (1987a) discussed the taxonomic history of the Anisophylleaceae, while van Vliet (1976) and Juncosa & Tomlinson (this volume) provided a detailed taxonomic background on the Rhizophoraceae (sensu lato). However, to place this contribution in perspective, a brief review follows.

Among modern systems, the genera of Anisophylleae have been included as a tribe in the Rhizophoraceae by Melchior (1964) and Takhtajan (1980), and by Thorne (1983) as a subfamily. Dahlgren (1983) and Cronquist (1983) recognized the separate family Ansiophylleaceae. In a review of the taxonomy and ecology of the Asian Rhizophoraceae, Hou (1958) included the genera of Anisophylleae. Prance et al. (1975) also followed this approach in a revision of Amazonian Rhizophoraceae. Van Vliet (1976), in a detailed analysis of the wood anatomy, concluded that the Rhizophoraceae comprise 18 genera arranged in four tribes (see Table 1), including the four genera assigned to the tribe Anisophylleae. Van Vliet (1976) concluded that wood-anatomical data provide no convincing case for excluding the Anisophylleae. This is no doubt partly due to the unusual amount of variation in the three tribes of the Rhizophoraceae s. str. In Table 1, we recognized a fifth tribe, Hypogyneae, which was separated from the tribe Macarisieae by Steyermark & Liesner (1983) on the basis of several morphological features (but cf. Juncosa and Tomlinson, this volume). Tobe & Raven (1987a) found that floral, seed, and embryo-

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TABLE 1. *Selected leaf characters of the genera of Rhizophoraceae and Anisophylleaceae.*[1]

	1. Phyllotaxy	2. Stipules	3. Margin	4. Margin glands	5. Venation type	6. Rank	7. Highest vein order	8. Areoles	9. Free endings	10. Tracheoids
Macarisieae										
Anopyxis	O	+	E	+	Eb	3r0	5–6	P	1–7	–
Blepharistemma	O	+	E, T	+	Eb	3r0–3r3	6–7	P	0–5	–
Comiphyton	O	+	E	+	E	3r1	6	P	0–2	–
Macarisia	O	+	E, T	+	E, Eb	2r0	6–7	P	0–3	F
Cassipourea	O	+	E, T	(+)	B, R	1r3-3r0	5–7	I	0–8	+, –
Sterigmapetalum	O	+	E	+	B	3r0-4r0	6	I	0–3	–
Gynotrocheae										
Carallia	O	+	E, T	+	B, E	1r2	5–7	I	0–6	F
Crossostylis	O	+	E, T	+	B, Eb	1r3–3r0	7	P	2–9	–
Gynotroches	O	+	E	?	E	3r0	7	I	0–9	–
Pellacalyx	O	+	E	+	Eb	2r3	6	P	3–10	–
Rhizophoreae										
Bruguiera	O	+	E	+	B	2r0–3r0	5–7	I	0–8	C
Ceriops	O	+	E	?	B	3r2	5–6	I	0–4	?
Kandelia	O	+	E	–	B	3r0	6	I	0–6	C
Rhizophora	O	+	E	–	B	3r0	6–8	I	0–4	?
Anisophylleaceae										
Anisophyllea	A	–	E	+	A, B	2r0–4r1	6–10	I	0–18	–, F
Combretocarpus	O	–	E	–	Eb	4r2	6	I	0–4	F
Poga	A	–	E	–	Eb	2r0	6–10	I	3–20	C
Polygonanthus	A	–	E	–	Eb	4r1	5	I	0–6	–

[1] Symbols used: 1. Phyllotaxy: O = opposite, A = alternate; 2. Stipules: + = present, – = absent; 3. Margin: E = entire, T = toothed; 4. Marginal glands: + = present, (+) = uncommon or doubtful, – = not detected; 5. Venation: A = acrodromous, B = brochidodromous, E = eucamptodromous, Eb = basally eucamptodromous and distally brochidodromous, R = reversed eucamptodromous; 6. Rank: e.g., 1r2 = first rank, second of three subranks (see Hickey, 1977); 7. Highest vein order present; 8. Areoles: P = polygonal, I = irregular; 9. Number of free vein endings per areole; 10. Tracheoids (terminal idioblastic sclereids): + = present, – = absent, F = few, C = common; 11. Marginal venation: F = fimbriate, I = incompletely looped, L = looped, Im = intramarginal vein; 12. Sclereids (diffuse): – = absent, A = astrosclereids; 13. Adaxial epidermis surface cell shape: P = polygonal, S = sinuous, I = interlocking, * = some larger cells present with radiating neighbors; 14. Hypoderm: + = present, – = absent; 15. Abaxial epidermis surface cell shape: P = polygonal, S = sinuous, I = interlocking, * = surface papillate; 16. Stomata: B = brachyparacytic, P = paracytic, C = cyclocytic, Ai = anisocytic, An = anomocytic, D = diacytic; 17. Fibers at veins: + = present; 18. Crystal type: D = druse, P = prismatic, S = crystal sand, – = absent; Crystal distribution: R = random, V = clustered along veins, Mv = along midvein only; Crystal frequency: A = abundant, Vc = very common, C = common, F = few; 19. Trichomes (simple): C = common, F = few, – = absent.

logical characters do not support segregation of this tribe.

The ordinal position of the 18 genera is even less agreed upon than the family composition. Melchior (1964) and Takhtajan (1980) assigned the Rhizophoraceae, including Anisophylleae, to the Myrtales. However, the consensus of the symposium on Myrtales at Sydney in 1981 (see Dahlgren & Thorne, 1984) was that the family should be excluded from that order. Cronquist (1983) retained the two families apart in his Rosidae with Anisophylleaceae in Rosales and Rhizophoraceae in the Rhizophorales. Dahlgren (1983) placed the Anisophylleaceae in the Corniflorae (Cornales) and the Rhizophoraceae in the Myrtiflorae (Rhizophorales). Thorne (1983) placed his Rhizophoraceae s. l. in the Corniflorae (Cornales). While a large literature has developed on various aspects of mangrove biology and management (see Rollet, 1981), the evolutionary relationships of the mangrove genera and their relatives remain much less studied.

Leaf architecture of samples of all genera of Rhizophoraceae and Anisophylleaceae is examined in this study to assess the contribution of foliar

TABLE 1. *Continued.*

11.	12.	13.	14.	15.	16.	17.	18. Crystal			19.
Marginal venation	Sclereids	Adaxial epidermis	Hypoderm	Abaxial epidermis	Stomata	Fibers at veins	Type	Distribution	Frequency	Trichomes
I, L	–	P	–	P	?	+	P	R, V	C	C
L	–	P	–	S	Ai, C	+	P	R, V	C	F
L	–	P	–	P	An, B	+	P	R	A	F
L	–	P	+	?*	?	+	P	R, V	Vc	–, C
L, I	–	P	–	P	B?	+	P	R, V	F, A	–, C
I, L	–	P	–, +	P	B, Ai	+	P	R, V	C, F	–
I, L	–	P*	–	P	B?	+	D	R	F	–
L	–	P	–	P	B, An	+	D	R, V	F, A	–
I, L	–	P	–	P	B, An	+	D	V	A	–
L	–	P	–	P	?	+	D	V	F	–
I, L	A, –	P	–	P	C	+	D	R, V	A	–
L	A?	P	–	P	C	+	D	R	A	–
L, F	–	P	–	P	C	+	S	R	C	–
L	A	P	+	P	C	+	D	R, V	C	–
I, L, Im	–	P, S, I	–	P, S, I	An, D, P	+	D	R, V	C, A	–
I, L	–	P	–	P	?	+	–	?	?	–
I	–	P	–	P	An, D, B	+	D	R, V	C, F	–
L	–	P*	–	P	P, An	+	–	?	?	–

characters to several taxonomic problems. Histological features detectable from cleared whole leaves are included in the observations. The leaf-architecture scheme developed by Hickey (1973, 1979), and later applied by Doyle & Hickey (1976), Hickey & Wolfe (1975), and Hickey & Doyle (1977) has supplied a practical basis for gathering and interpreting these data in an evolutionary context. In addition, we have reviewed the wood-anatomical data from the comprehensive studies of Marco (1935) and van Vliet (1976). Using these data we will assess the intergeneric variability, the degree to which tribal groupings can be supported, and whether the exclusion of Anisophylleaceae from Rhizophoraceae can be sustained. These are the easier tasks. More complex is an assessment of the position of the Ansiophylleaceae among the angiosperms.

MATERIALS AND METHODS

The leaf sample, including 53 specimens representing all 18 genera, was obtained from the herbaria of the Missouri Botanical Garden (MO), Paris (P), and some individual collectors. In addition, descriptions were amplified after inspecting all Rhizophoraceae slides deposited in the National Cleared Leaf Collection currently deposited at the Peabody Museum of Yale University. All specimens are cited following generic descriptions.

All of the leaves were studied as safranin-stained clearings. The permanent specimens prepared for this study were cleared in 5% NaOH followed when necessary by 5.25% $NaHCO_3$ (commercial laundry bleach). Chloral hydrate was avoided, as it tends to destroy the differential stainability of venation. The clearings were dehydrated to 95% ethanol, stained in 0.5% safranin-O in 95% ethanol, dehydrated to toluene, and mounted between glass plates in cover glass resin. Hickey's (1979) descriptive protocol was followed. Leaf rank on a scale of 1–4 with three subdivisions within each rank, as presented by Hickey (1977 and pers. comm.), was scored for each specimen. The term "domain" is used to denote the area bounded by veins of a given rank, except that intercostal area is used instead of "secondary domain." The shape of intercostal areas and higher-order domains is a useful measure of the regularity of architectural organization (Hickey, pers. comm.).

Except where descriptions from other literature are specifically noted, all of the descriptions given here and used for discussions and conclusions are restricted to the specimens cited. No claim is made that the sample observed encompasses all of the variation, particularly in the larger genera.

OBSERVATIONS

Anisophyllea R. Br. ex Sabine (Figs. 32–39)

Leaves are chartaceous to membranaceous, entire, markedly asymmetrical in most species, ovate on one side, elliptic to obovate on the other. Those of *A. pomifera* are symmetrical and suborbiculate. Vincent & Tomlinson (1983) described the marked dimorphy in *A. disticha*. Venation is acrodromous, basal or suprabasal; the primary vein is slightly curved and is the same size as or larger than the acrodromous secondaries. Secondaries are perfect, extending more than ⅔ the distance toward the apex. Simple intersecondaries are present or absent. The uniformly curved secondaries originate from the primary at a narrow or wide acute angle, the upper more obtuse or acute than the lower. Tertiaries are percurrent and forked or unforked and may be acute or perpendicular to the primary vein; angle of origin is acute or right, exmedially or admedially to the secondaries. Quaternary veins may be percurrent or not and are random orthogonal to the tertiaries. Stomata appear to have 2 large paracytic guard cells surrounded by 8–10 smaller epidermal cells with radiating anticlinal walls. The margin in *A. meniandii* has shallow convex glands that are not approached by any larger veins. Minor veins in the area often have tracheoidal endings but do not closely approach the gland. Other species have no detectable glands.

Specimens examined. *Anisophyllea apetala* King: SARAWAK. *Clemans & Clemans 21596* (MO). *A. boehmii* Engl.: Burundi, *Reekmans 2686* (MO). *A. cinnamomoides* (Gardner & Champ.) Alston: Sri Lanka, *Meijer 1709* (MO), *Macnae s. n.* (1968) (US; LJH 1855). *A. disticha* (Jack) Baillon: Sumatra, *Toroes 2610* (US; LJH 1856); Borneo, *Elmer 20409* (MO). *A. griffithii* (Jack) Baillon: North Borneo, *Anderson 4290* (MO). *A. meniandii* Aubrév. & Pellagrin: Liberia, *Jacques-Georges 25941* (MO). *A. poggei* Engl. ex De Wild & T. Durand: Congo, *Makany 1054* (MO). *A. pomifera* Engl., Malawi, *Pawek 7414* (MO).

Anopyxis (Pierre) Engl. (Figs. 1, 2)

Leaves are symmetrical, oblanceolate, with an attenuate apex and cuneate base. The texture is membranaceous and the margin entire. The eucamptodromous pattern tends toward brochidodromy distally. The primary vein is moderately thick and straight. Secondary veins have a widely acute divergence, are uniform base to apex, and curve uniformly toward the margin. Long sinuous intersecondaries are common. Tertiary veins are acute exmedially and right or obtuse admedially. They are often percurrent with intersecondaries and, distally, with secondaries. Tertiary veins are generally oblique to the primary vein. Quaternary and quinternary veins produce orthogonal domains of irregular shape. The polygonal islets are often formed in interquinternary domains. Occasional marginal glands are vascularized by short straight veins that originate on a secondary arch. The gland is a shallow mound on the edge of the entire margin.

Specimen examined. *Anopyxis calaensis* Sprague: Nigeria, *Kennedy 1561* (MO).

Blepharistemma Wall. ex Benth. (Figs. 3–6)

The leaf is symmetrical and elliptic, obovate, or lanceolate with an acute apex and an acute or obtuse base. Texture is chartaceous or membranaceous. The margin is shallowly toothed in *B. corymbosum* or entire in *B. membranifolia*. Eucamptodromous secondaries originate from the straight primary vein at a uniform wide acute or acute angle. In the distal half of *B. membranifolia* the secondaries are brochidodromous. Occasional simple intersecondaries are present and may be exmedially forked. Tertiary veins are sinuously percurrent, often forked, forming polygonal domains with intersecondaries. Tertiary angles of origin are variable, but the tertiaries tend to be oblique to the primary vein. They originate mostly orthogonal to the secondaries but may be exmedially acute. Quaternaries and quinternaries form irregular orthogonal domains. Teeth are shallow, strongly asymmetric, and curved inward to a small concave sinus. An asymmetrical turbinate gland having a superficial columnar epidermis protrudes from the apex parallel to the margin or incurved toward the sinus. A single vein the diameter of a secondary originates from a secondary arch and curves apically to the sinus, ending in the tooth apex, just below the gland. Just inside the margin, tertiary and quaternary veins branch off from the tooth vein and become part of the looped marginal venation.

Specimens examined. *Blepharistemma corymbosum* Wall. & Benth.: India, *Metz 713* (P). *B. membranifolia* (Miq.) Ding Hou: India (CAZ).

Bruguiera Lam. (Fig. 27)

Leaves are coriaceous or chartaceous, entire, symmetrical, elliptic or oblong, with an acute apex and base. Venation, not easily seen, is brochidodromous with tertiary and quaternary arches or with a tendency toward a strong (sub)marginal secondary collector vein. Secondaries diverge from the stout, straight primary vein at a wide-acute to acute-decurrent angle and meet the superadjacent secondaries at an obtuse or right angle. The upper secondaries may be more obtuse than the lower. Intersecondaries are simple or composite and are often admedially ramified or "perfect admedially." Tertiary arches may enclose the secondaries and form an intramarginal vein. Tertiaries originate from either side of the secondaries at acute, right, or obtuse angles. Tertiaries may be randomly forked and may form large polygonal domains elongated parallel to the secondaries. Quaternary veins have a random polygonal relationship to the tertiaries. The margin has occasional shallow glands, obscurely vascularized in the existing preparations.

Specimens examined. *Bruguiera gymnorrhiza* (L.) Lam.: cultivated (FTG) [RCK 1443]; Ryukyu Islands, *Kokuhara & Sunagawa 83* (US; LJH 1851). *B. parviflora* (Roxb.) Wright & Arn.: Australia, *Blake 16995* (US; LJH 1852).

Carallia Roxb. (Fig. 21)

Leaves are chartaceous to membranaceous, symmetrical, entire or toothed, elliptic, obovate or ovate, mucronate or acute at the apex and acute to decurrent at the base. Venation is brochidodromous or eucamptodromous basally and brochidodromous distally. Secondary veins diverge at a narrow or wide acute angle from the straight primary, at a uniform angle, or more widely acute angle approaching the apex. Secondaries in brochidodromous segments join the superadjacent secondaries acutely and may be enclosed by tertiary and higher-order arches. Tertiaries may diverge at right angles or be acute exmedially and obtuse admedially. Tertiaries ramify randomly and may be retroflexed; the branches are sometimes aligned with the secondaries and intersecondaries. Intersecondaries are basally simple, distally composite, or forked. In *C. brachiata*, intersecondaries evenly divide the intercostal areas and join the superadjacent secondary high in the intercostal area. Teeth in *C. fascicularis* are acuminate, closely spaced, and are basally and distally concave. Veins originate from eucamptodromous arches (tertiary and higher sized) and enter the teeth symmetrically. They pass off higher-order loops and veinlets obtusely, forming garland connections below the teeth. *Carallia brachiata* had no expressed teeth but regular, papillate, nonstaining glands. Vascularization is often by an approaching marginal loop or several small anastomosing veins that often flare just below the gland. Hou (1958) reported the teeth to be dense in juvenile leaves and quite variable for the genus in general.

Specimens examined. *Carallia brachiata* (Lour.) Merr.: Hainan, China, *Lau 488* (MO); Indochina, *Pierre 683* (A, MO). *C. fascicularis* Guillaumin: Cochinchina, *Poilane 116* (US; LJH 1848). *C. integerrima* DC.: India, *Saldana 15267* (US; LJH 1850). *C. lucida* Roxb.: Burma, *Gallatly 783* (US; LJH 1849).

Cassipourea Aubl.
(Figs. 13–16, 19, 20)

The leaf is symmetrical and elliptic to wide ovate (to orbiculate in *C. rotundifolia*). Texture is chartaceous to coriaceous, and the margins are entire or shallowly toothed. The straight primary vein is attached to brochidodromous secondaries, which in turn pass off tertiary and quaternary loops. Secondary arches attach to superadjacent secondaries at acute, right, or obtuse angles. In *C. rotundifolia*, the venation pattern is reverse eucamptodromous with retroflexed secondaries. Secondary veins have a wide-acute, uniform angle of origin from the primary vein. They form regular intercostal areas. Intersecondaries are simple, short, and forked, or long, then extending to the secondary arches. There may be several per intercostal area. Tertiary veins are obtuse or random admedial to the secondaries, and acute or random exmedially. Tertiaries are forked and not often percurrent. Tertiary domains are irregularly polygonal, with several extending across an intercostal area. Quaternary veins originate randomly, forming irregular, well- or poorly defined domains. Teeth are very shallow with a slightly convex glandular surface that may have a tuft of simple trichomes. No sinus is distinguished distal to the apex. Teeth are vascularized by a single arching vein originating from a secondary arch. As the vein curves apically toward the tooth, it passes off tertiary and quaternary loops. No marginal glands were detected in *C. ceylanica*.

Specimens examined. *Cassipourea brittoniana* Fawcett & Rendle: Jamaica, *Award & Proctor 14422* (GH, US: LJH 1198). *C. barteri* (Hook. f.) N. E. Br.: Cote d'Ivoire, *Chevalier 19981* (P); *C. ceylanica* (Gardn.) Alston: Sri Lanka, *Mueller et al. 69042737* (MO); Sri Lanka, *Cooray 70040204R* (US: LJH 1854). *C. elliptica* Poir.: British Honduras, *Schipp 254* (GH; LJH 1302). *C. guianensis* Aublet: Puerto Rico, *Liogier 10575* (GH; LJH 1199); Brazil, *Dahlgren & Sella 86* (US: LJH 1853). *C. gummiflora* Tul. var. *gummiflora*: Madagascar, *Boivin s.n.* (1851) (P). *C. peruviana* Alston: Peru, *Croat 20518* (MO); Peru, *Klug 2235* (GH: LJH 1301). *C. rotundifolia* (Engl.) Alston, Tanganyika, *Schlieben 3552* (GH; LJH 1303).

Ceriops Arn. (Figs. 28, 29)

Leaves are coriaceous, entire, symmetrical, oblong, with a rounded apex and an acute, decurrent base. Venation is obscure, brochidodromous. Secondaries diverge from the straight primary moderately acutely, the upper ones somewhat more obtuse than the lower. Secondary arches join the superadjacent secondaries obtusely. Intersecondaries are simple, equally dividing the intercostal areas. Tertiary veins originate at obtuse or right angles admedially and exmedially and may be admedially ramified. Quaternary veins branch from transverse tertiaries and run parallel to the secondaries. Occasional convexities in the margins do not look glandular and are not obviously vascularized.

Specimens examined. Ceriops boiviniana Tul.: Madagascar, *Gentry 11901* (MO: LJH 4512); Comoro Isl., *Lorence 2872* (MO).

Combretocarpus Hook. f. (Fig. 40)

Leaves are membranaceous, entire, symmetrical, elliptic, with an obtuse apex and acute base. Secondaries arising from the straight primary vein are brochidodromous distally and eucamptodromous basally. Secondaries arise at a uniform, narrowly acute angle and are uniformly concave. The brochidodromous secondaries join superadjacent secondaries at right angles. Simple intersecondaries are present. Tertiary veins are percurrent and arise from both sides of secondaries at right angles. Tertiaries are oblique to the midvein at a uniform angle. Quaternary veins are orthogonal to tertiaries. Looped venation is typical at the margin but a straight collector vein may be present. No teeth or marginal glands were detected.

Specimen examined. Combretocarpus rotundatus (Miq.) Danser: North Borneo, *van Niel 4271* (MO).

Comiphyton Floret (Figs. 7, 8)

Leaves are symmetrical, narrowly oblong, with an acuminate apex and obtuse base. Texture is membranaceous, and margins are entire. Eucamptodromous secondaries arise from a straight primary vein at a moderately acute divergence angle with the upper veins more obtuse than the lower ones. The secondaries are uniformly curved with lower secondaries being longer and more strongly ascending. The few short intersecondaries are exmedially forked. Tertiary veins are sinuously percurrent and oriented at approximately right angles to the primary vein, especially the outer ones. They are acute exmedially and obtuse admedially. Quaternary and quinternary veins arise orthogonally and form irregular polygonal domains. No teeth are expressed, but shallow, marginal, domelike glands are present. Short, single veins arise from secondary or tertiary loops and end directly below a gland. The leaf venation drawings of Floret (1974) agree with my observations.

Specimen examined. Comiphyton gabonensis J. J. Floret: Gabon, *Le Testu 5918* (P).

Crossostylis Forster & G. Forster (Fig. 23)

Leaves are chartaceous, entire or toothed, symmetrical, wide oblong to narrow obovate, with an acute or obtuse apex and an acute to subdecurrent base. Venation is brochidodromous or sometimes basally eucamptodromous. Secondaries arise with a narrow- or wide-acute divergence from the straight primary vein. Secondaries are uniformly curved, join the superadjacent secondaries at right angles, and are enclosed by tertiary and quaternary arches. Tertiary veins are usually forked, originating at random angles. Quaternary and quinternary veins form irregularly polygonal domains and are often retroflexed. Teeth are shallowly crenate with a fine glandular apiculum. A single, conspicuous tooth vein originates at a secondary or higher-order arch, which becomes smaller in diameter distally. Smaller veins of the marginal reticulum attach decurrently to the tooth vein.

Specimens examined. Crossostylis biflora Forster: Samoa, *Veupel 493* (US: LJH 2256); Tahiti, *Balgooy 1715* (MO); *C. multiflora* Brongn. & Gris.: New Caledonia, *McPherson 2344* (MO).

Gynotroches Blume (Fig. 24)

Leaves are chartaceous, entire, elliptic with an acuminate apex and an acute base. Venation is eucamptodromous with secondaries uniformly curved after diverging at a wide acute angle from the straight primary. Intersecondaries are admedially simple and exmedially composite. Tertiary veins are acute exmedially, obtuse admedially, and admedially and transversely ramified. Quaternaries and quinternaries are polygonal to irregular. Uncommon marginal, glandlike, shallow protuberances are not consistently vascularized. An enlarged vein may end in the vicinity, but it may not originate as deeply as a secondary or tertiary arch.

Specimens examined. Gynotroches axillaris Blume: Philippines, *Wenzel 1323* (MO); MO 2227076 (MO).

Kandelia Wight & Arn. (Figs. 30, 31)

Leaves are chartaceous, entire, symmetrical, obovate, with an obtuse apex and an acute base.

Venation is obscure, brochidodromous, with secondaries arising at a moderately acute angle from the straight primary vein. Upper secondaries are more obtuse than lower secondaries. Secondary arches join the superadjacent secondaries at right or obtuse angles. Simple or composite intersecondaries are present. Tertiary veins diverge from secondaries at right angles from both sides and may be transversely ramified. No marginal glands were detected.

Specimens examined. *Kandelia candel* (L.) Druce: Taiwan, *Murata & Nishimura 31214* (MO); Taiwan, *Peng 6042* (MO).

Macarisia Thouars

Leaves are symmetrical or asymmetrical, elliptic to suborbiculate. The apex is emarginate, or rounded, or acute or acuminate, and the base is acute to decurrent. The texture is chartaceous or coriaceous and the margin entire or shallowly toothed. Eucamptodromous secondary veins diverge moderately acutely and uniformly from the straight primary vein. They are gradually apically curved and unbranched. Secondaries in the distal half of the leaf may be brochidodromous. The few intersecondaries are short and ramify into tertiaries. Tertiary veins may be sinuously percurrent, and connections to secondaries are at right angles or variable. In *M. lanceolata* the tertiaries are admedially obtuse and exmedially acute. Tertiaries are oriented relatively uniformly at right angles to the primary vein. Quaternary veins are orthogonal to tertiaries, forming irregular polygonal domains. Higher-order veins are indistinguishable in a reticulum. Areole veinlets often anastomose to form smaller suspended islets within an areole. Teeth are shallow, and strongly asymmetric; they have rounded convex bases leading to shallow, rounded, concave sinuses above the glandular apex. The turbinate gland points apically and is surrounded by a tuft of simple trichomes. A single vein originates from a secondary arch and curves toward the tooth apex where it flares slightly. It does not supply the sinus. Tertiary and smaller veins that form marginal loops or the submarginal reticulum merge decurrently or randomly with the tooth vein.

Specimens examined. *Macarisia lanceolata* Baillon: Madagascar, *Capuron 11.339SF* (MO). *M. pyramidata* Thouars: Madagascar, *Serv. Forestier 11R460* (MO); Madagascar, *Dorr 4495* (MO).

Pellacalyx Korth. (Fig. 22)

Leaves are chartaceous, entire, symmetrical, oblong, with an acuminate apex and an obtuse base. Venation is eucamptodromous basally and looped brochidodromous distally. Uniformly curved secondary veins diverge from the straight primary at a uniform, widely acute angle. Secondaries are enclosed by tertiary and higher-order arches. Intersecondaries are short, admedially simple, and exmedially composite. Tertiary veins are transversely ramified and originate from secondaries acutely, both admedially and exmedially. Quaternary and quinternary veins are random. Depressions in the leaf margin contain round, flat-topped glands. A single strong vein arises from a tertiary eucamptodromous loop and ends just at the margin below each gland.

Specimen examined. *Pellacalyx frustulata* Merr.: Philippines, *Wenzel s.n.* (1915) (MO).

Poga Pierre (Figs. 42, 43)

Leaves are chartaceous or membranaceous, entire, symmetrical, elliptic, oblong or lorate, with an acuminate or emarginate apex and an acute base. Venation is brochidodromous with tertiary and higher-order arches, or eucamptodromous at the base becoming brochidodromous distally. The straight or curving primary vein, often distally forked, produces secondaries at a wide acute angle, with upper secondaries often more obtuse than the lower. Secondary arches join the superadjacent secondaries at acute angles. Intersecondaries are simple at the primary vein, becoming composite exmedially. Tertiary veins are sinuous and obliquely percurrent, joining secondaries or intersecondaries. Tertiaries arise at acute angles admedially from secondaries and at right angles exmedially, or their course may be irregular. Quaternary veins are random, often retroflexed, forming incomplete domains. Quinternary veins may be retroflexed in any orientation. No marginal glands were detected.

Specimens examined. *Pogo oleosa* Pierre: Cameroon, *Zenker s.n.*, (1909) (US: LJH 1858); Nigeria, *Ariwaodo s.n.* (1983) (FHI).

Polygonanthus Ducke (Fig. 41)

Leaves are membranaceous, entire, elliptic, with an acuminate apex and an asymmetric, acute base. Eucamptodromous secondaries arise at a wide acute angle from the straight primary vein. A few of the ascending secondaries connect brochidodromously. Some dominant secondaries show an incipient suprabasal acrodromy. Simple intersecondaries are long, robust and common. Tertiary veins are straight, percurrent, and oblique to the midvein at a constant angle. Tertiaries diverge at right angles from both sides of secondaries. Quaternary veins form regular polygonal domains, often elongated parallel to the secondaries. Quinternary veins arise randomly from lower-order veins. No marginal glands were detected. At the leaf tip, the midvein ends at the margin similarly to tooth vasculature in the Macarisieae.

Specimen examined. Polygonanthus amazonicus Ducke: Brazil, *daSilva 4486* (MO).

Rhizophora L. (Figs. 25, 26)

Leaves are coriaceous, entire, symmetrical, oblong or elliptic with an obtuse apex and an acute base. Venation is brochidodromous, and the secondary arches may form a strong composite collector vein. Secondaries diverge from the straight primary at a right or acute (decurrent) angle. The divergence angle is uniform, or the upper and lower secondaries may be more acute than the middle sets. Secondary arches join superadjacent secondaries at acute, right, or obtuse angles. Intersecondaries are absent or simple and arising from primary veins or from secondary loops; they are obmedially ramified parallel to the secondaries. Tertiaries arise at a right angle from both sides of secondaries, are not percurrent, are often orthogonal with intersecondaries, and often are admedially ramified forming a random reticulum with no directional orientation to the primary vein. No marginal glands were detected.

Specimens examined. Rhizophora mangle L.: Florida, *Curtiss 5438* (US: LJH 1846); Hawaii, *Degener & Wielbese 3363* (MO). *R. mucronata* Lam.: Caroline Isl., *Anderson 1049* (US: LJH 1847). *R. stylosa* Griffith: Australia, *Gill 220-4* (MO).

Sterigmapetalum Kuhlm. (Figs. 17, 18)

The leaves are symmetrical, oblanceolate or elliptic, with an acute or emarginate apex and a rounded to acute decurrent base. The leaves are entire-margined and chartaceous. Venation is looped brochidodromous, and secondaries have an acute to wide acute divergence from the straight primary vein. Secondaries are uniformly spaced with the arches fusing with the superadjacent secondaries at obtuse or right angles. Composite intersecondaries may be present. Tertiary veins originate mostly at right angles exmedially and admedially, and are oblique to the primary vein at a constant angle. Tertiaries are forked percurrent, producing irregular but evenly sized domains. Quaternary veins are orthogonal to tertiaries. Quaternary and higher-order loops festoon the secondary arches. Veinlets in the areoles often anastomose to form small suspended islets. Rarely a flattened marginal gland is found that may be directly vascularized by a single vein arising from a tertiary loop. The illustration of leaf architecture by Steyermark & Liesner (1983) agrees with these observations.

Specimens examined. Sterigmapetalum guianense Steyerm. subsp. *ichunense* Steyerm. & Liesner: Venezuela, *Liesner 7314* (MO); Venezuela, *Clark 7275* (MO).

DISCUSSION

VENATION PATTERNS

Brochidodromy and eucamptodromy appear to be quite closely related since intermediate forms are often found. In intermediate leaves, the distal secondary veins are always brochidodromous and the proximal secondary veins always eucamptodromous. The ontogeny of lamina tissue in many dicot leaves begins with the blocking out of the distal portion of the lamina, while the proximal portion is produced later following intercalary growth of the midrib. In early developmental stages of *Fuchsia* and *Hauya* (Onagraceae; Keating, unpubl.), brochidodromous leaves appear to have more or less simultaneous lamina inception with unified marginal growth. The cross attachment of secondary arches to the superadjacent secondaries occurs as the marginal expansion is slowing down. In eucamptodromous leaves, the later basipetal inception of secondaries on the midrib is followed by an acropetal marginal expansion of the lower lamina. This produces apically arching secondaries that eventually dissipate in submarginal loops parallel to the margin.

Transitions between distal brochidodromy and basal eucamptodromy are commonly found in *Anopyxis*, *Carallia*, *Crossostylis*, and *Pellacalyx* of the Rhizophoraceae, as well as *Combretocarpus*, *Poga*, and *Polygonanthus* of the Anisophylleaceae.

The developmental transition from brochidodromy to eucamptodromy suggests a phylogenetic recapitulation, but further, it is certainly clear that the two venation patterns are closely related with eucamptodromy always appearing later in development. The data of Hickey & Wolfe (1975) show that brochidodromy is stratigraphically earliest, and it tends to have the lowest rank order (organizational complexity and regularity) of any type of angiosperm venation pattern.

Rhizophoreae, having the most coriaceous leaves, are exclusively brochidodromous with well-developed secondary arches meeting the superadjacent secondaries at an obtuse angle. These arches have tended to become straightened, forming a submarginal collector vein, a tendency shown by no other tribe. This implies a leaf ontogeny with little if any basal acropetal expansion. Instead, it can be hypothesized that the leaves have a uniform marginal expansion, followed by a more abrupt cessation of expansion and a more synchronized final marginal differentiation.

Tertiary veins in the Rhizophoraceae generally do not show predictable patterns in most genera. They are generally forked, not percurrent, and have irregular domains. Branching from secondaries is acute to obtuse and seldom sufficiently well developed to be called orthogonal, or regularly polygonal.

Areolation is most commonly imperfect, although it may be well developed in *Blepharistemma*, *Comiphyton*, and *Macarisia* of the Macarisieae, and in *Combretocarpus* of the Anisophylleaceae. Free vein endings are variable within each tribe but generally fewer than seven. The highest number, to greater than 20 in *Anisophyllea*, is large for both families.

The most distinctive pattern of secondary architecture is found in *Anisophyllea*, most species of which show basal and suprabasal acrodromy (Fig. 32). Some species (*A. griffithii*, Fig. 33, and a specimen of *A. pomifera*) are not acrodromous but rather eucamptodromous with irregular spacing of the pinnate secondaries on the midvein. All specimens of the other three genera of Anisophylleaceae are eucamptodromous, often with distal brochidodromy. *Polygonanthus* has some secondaries that show the tendency toward strong ascending curvature parallel to the margin as seen in *Anisophyllea*.

MARGINAL TEETH AND GLANDS

As leaf teeth in the Rhizophoraceae are best developed in the Macarisieae, we will refer to them as the Macarisioid type. The teeth are best developed and largest in *Blepharistemma* (Figs. 3–5), although conspicuous expression can also be found in the genera *Macarisia* (Figs. 10–12), *Cassipourea* (Figs. 13, 14), and in *Carallia* of the Gynotrocheae. In Macarisieae, the teeth are markedly asymmetric, having a gently convex margin proximal (basal) to the tooth apex. The apex is incurved facing directly onto an abruptly or gradually concave sinus.

Tooth vascularization is always by a single vein usually originating from an ascending secondary vein or tertiary loop. It may begin below the tooth and curve gradually toward the apex, entering the tooth symmetrically (Figs. 11, 12). In other cases, the vein originates directly opposite the tooth apex and follows a straight course toward the distal margin of the tooth, supplying the sinus as well as the apex (*Blepharistemma*, Fig. 5). The tooth vein is usually more strongly developed than the neighboring veins, which often join it oriented randomly or decurrently. The tooth vein ends slightly flared at the margin, which is surmounted by a turbinate, rounded or flattened gland. On expressed teeth, glands are often incurved toward the sinus. They often show no stainability and often have a surface of columnar cells. No visible epithem appears within the lamina distal to the vein. On leaf margins with glands but no expressed teeth, the relationship between veins and glands is not basically different from those leaves with expressed teeth.

Carallia fascicularis shows an unusual tooth for the family. It is concave on both sides, very frequent and conspicuous, and is vascularized by one vein with tertiary garland connections to the neighboring tooth veins.

Lersten & Curtis (1974) reported on the structure of colleters as found at the base of stipules in *Rhizophora mangle*. They are not regularly associated with vascularization, and they appear from the evidence presented to have no obvious relationship to glandular teeth in other genera of the family.

Within the available data, there are no strong correlations between the degree of expression of glands and teeth with the habit or habitat. It can be noted in general that the four specialized mangrove genera have more coriaceous leaves than the inland genera. Givnish (1979) reviewed the statistical data showing a correlation between toothed (nonentire) leaves and a thin, noncoriaceous lamina. He also noted that deciduous leaves are toothed more frequently than evergreen leaves. If the ancestors of Rhizophoraceae were thin-leaved and possibly from seasonal habitats, the nontoothed leaves are clearly derived. On the other hand, the best-developed teeth are found only on plants with eucamptodromous venation, while brochidodromous leaves have very reduced teeth/glands or no marginal features at all. Hickey & Wolfe (1975) presented stratigraphic evidence that the brochidodromous pattern is primitive in angiosperms. While it is tempting to regard teeth in Rhizophoraceae as a reduction series, this cannot be taken as proven.

EPIDERMIS AND STOMATA

The paradermal outline of the anticlinal walls of epidermal cells is not particularly useful systematically in these genera. In nearly all specimens, cells are polygonal (isodiametric or elongated up to 2:1 length/width ratios) and are the same on both surfaces. *Blepharistemma* has sinuous abaxial epidermal cells, *Macarisia* and *Poga* have papillate abaxial epidermal surfaces. *Anisophyllea* species vary in cell outline from polygonal to undulate to interlocking shapes with the two surfaces matching or not. In some genera, occasional larger rounded cells occur that have more radiating neighbors than most of the smaller cells. Such large cells were found in *Carallia* and *Pellacalyx* of the Gynotrocheae, and in *Anisophyllea* and *Polygonanthus* of the Anisophylleaceae.

Observations on stomatal types are difficult in some cases, as they may be quite obscure in clearings. Nevertheless, a few conclusions seem valid. The Rhizophoreae are quite distinct with their apparently cyclocytic patterns (Figs. 27, 29, 31). The subsidiary cells appear narrow and differentiated from other epidermal cells. They vary in number from 5 to 8–10 cells surrounding the guard cells. Stomata are exclusively abaxial in all genera observed. While the brachyparacytic pattern is most common in all other genera of both families, anomocytic and anisocytic types were noted as well.

IDIOBLASTIC CELLS

The Macarisieae and Hypogyneae are distinguished by having prismatic crystals with small druses rarely present (*Blepharistemma*). All other genera studied have only druses, no prismatics. Occasional specimens have no crystals. Druses in the Rhizophoreae are normally birefringent but have centers that appear dark or extinct under polarized light. This phenomenon was also noted in *Pellacalyx*, a genus otherwise clearly belonging to Gynotrocheae.

In the Gynotrocheae, druses tend strongly to cluster along veins with only a few scattered randomly in the mesophyll. In other tribes, the distribution of crystals varies among the genera. Crystals may cluster nonexclusively at the veins, and many are scattered randomly. In this respect, the Anisophylleaceae are unexceptional.

Foliar sclereids of several types were noted in this study in both families. A series of studies by Rao & Bhattacharya (1978), Rao et al. (1978), and Rao & Das (1979) have also called attention to these cell types, particularly in the tribe Rhizophoreae. "Diffuse polymorphic sclereids" (Rao et al., 1978), here called astrosclereids, are found in *Bruguiera*, *Ceriops*, and *Rhizophora* (Figs. 25, 26) of the Rhizophoreae and in *Pellacalyx* of the Gynotrocheae. A second type, the terminal tracheoid, is characteristic of *Macarisia*, *Cassipourea*, *Crossostylis*, *Bruguiera*, and *Kandelia* (Fig. 30) of the Rhizophoraceae, as well as in *Anisophyllea*, *Combretocarpus*, and *Poga* (Fig. 43) of the Anisophylleaceae. Only in Rhizophoreae are astrosclereids and terminal tracheoids commonly found together.

FAMILY AND TRIBAL DELIMITATION: RHIZOPHORACEAE

A review of the available leaf-architectural and histological data (Table 2) demonstrates much overlap in most features and an apparent relatedness among all of the genera. Yet a few characters readily distinguish the tribes. The Macarisieae and Hypogyneae have prismatic crystals in the leaves, and the Hypogyneae are further differentiated by having mostly looped brochidodromous leaf venation instead of mostly eucamptodromous as found in the Macarisieae.

In several genera of the Macarisieae (*Anopyxis*, *Blepharistemma*, *Comiphyton*, *Macarisia*), the leaf-rank organization is unusual: the tertiary veins and areolation show a high level of organization while the secondaries are less well organized. Normally, rank order increases proceed in ascending order from secondaries through tertiaries to the organization of areoles (Hickey, 1977). Following current practice (Levin, 1986; Hickey, pers. comm.) we have ranked the leaves according to the highest level obtained so that the maximum evolutionary advancement is reflected in the classification. In his study of the leaf architecture of Euphorbiaceae: Phyllanthoideae, Levin (1986) hypothesized that venation where secondaries are less well organized than tertiaries represents a regression of rank order. He found this type among leaves from arid, arctic, and alpine habitats. What its significance is in the Macarisieae remains obscure, as these genera do not face such environmental stresses.

The Gynotrocheae and Rhizophoreae are distinguished from the Macarisieae by having druses in the leaves. The Rhizophoreae have coriaceous leaves with brochidodromous venation and a cyclocytic stomatal pattern unique in the family. Also, three of the four genera in this tribe have astrosclereids in the leaves. The Gynotrocheae have chartaceous leaves and brachyparacytic or other noncyclocytic stomata. In many respects the Rhizophoreae are the most unified and specialized group of genera due to their mangrove habit, vivipary, chromosome morphology (Yoshioka et al., 1984), bijugate phyllotaxy (Tomlinson & Wheat, 1979), and the leaf

TABLE 2. *Summary of leaf characters of the Anisophylleaceae and tribes of Rhizophoraceae.*

	Macarisieae	Hypogyneae	Gynotrocheae	Rhizophoreae	Anisophylleaceae
Shape	elliptic, obovate, oblanceolate, suborbiculate, symmetrical, or asymmetrical	elliptic, oblanceolate, ovate (wide or narrow) orbiculate	elliptic, obovate, ovate (often narrow)	elliptic, occasionally obovate	elliptic, suborbiculate, symmetrical or asymmetrical
Apex	acuminate to emarginate or rounded	acuminate to emarginate or rounded	acuminate to obtuse	acute to obtuse	acuminate to rounded or emarginate
Base	decurrent, acute to obtuse	decurrent, acute to rounded	decurrent, acute to occasionally obtuse	decurrent to acute	decurrent to acute or rounded
Margin	toothed or entire	toothed or entire	toothed or entire	entire	entire
Texture	membranous or coriaceous	chartaceous or coriaceous	chartaceous	chartaceous or coriaceous	chartaceous
Primary vein	straight; normal to enlarged	straight; normal	straight; normal to enlarged	straight; normal to enlarged	straight; normal; one to several
Secondary type	eucamptodromous to distally brochidodromous	looped brochidodromous to brochidodromous; one reverse eucamptodromous	brochidodromous, eucamptodromous to distally brochidodromous	brochidodromous	brochidodromous, eucamptodromous, acrodromous
Secondary vein origin	wide to narrow acute	wide to medium acute	wide to narrow acute	wide to narrow acute	basal to suprabasal and strongly ascending to wide acute
Intercostal areas	regular or irregular	regular, occasionally irregular	regular or irregular	mostly regular	regular or irregular
Rank order	2r0–3r1	1r3–4r0	1r0–3r0	2r0–3r2	2r0, 4r1
Intersecondaries	short, forked to long, sinuous	simple or composite long or forked	simple or composite often forked	simple or composite often obmedially ramified	none, few, or common; short, long; simple to distally composite
Tertiary veins	random angle; sinuous percurrent or forked	acute to obtuse angle; forked or percurrent; occasionally parallel to secondaries	right to obtuse admedially; right to acute exmedially transverse or parallel to secondaries; ramified or forked	usually right admedially & exmedially; occasionally obtuse or acute	right or acute; sinuous or forked percurrent; mostly alternate

TABLE 2. *Continued.*

	Macarisieae	Hypogyneae	Gynotrocheae	Rhizophoreae	Anisophylleaceae
Tertiary domains	irregularly polygonal	irregular or regular polygonal	irregular	irregularly polygonal; occasionally parallel to secondaries	irregular polygonal
Highest order	5–7	5–7	5–7	5–8	5–10
Areole development	mostly imperfect, few well developed	imperfect to well developed	incomplete to imperfect	incomplete, imperfect to well developed	incomplete, imperfect to well developed
Areole shape	irregular, polygonal	irregular to polygonal to rectangular	irregular; occasionally polygonal	irregular to polygonal	irregular to polygonal
Free endings	0–2, 1–7, 1–5	0–2, 0–8, mostly < 0–4	1–3, 0–6, 2–9, 3–10	0–4, 0–8	0–2, 3–9, 10–18, 15–> 20
Tracheoidal endings	none	to 70% only in *Cassipourea ceylanica*	none	none or common	none to few to > 50%
Marginal venation	looped; occasionally incompletely looped	looped or incompletely looped	looped or incompletely looped	looped or incompletely looped	looped to incompletely looped; often intramarginal vein
Crystal type	prismatics, rare druses	prismatics	druses, small to medium	druses, sand and small prismatics	druses
Distribution	along veins or random in mesophyll	along veins or random in mesophyll; occasional in epidermis	along veins; random mesophyll or epidermis	along veins, random mesophyll	along veins, random mesophyll
Adaxial epidermis shape	polygonal	polygonal	polygonal; occasionally larger rounded cells	polygonal	polygonal to undulate to interlocking; occasionally large centered cells
Length/width ratio	1–1.5:1	1–2:1	1–2:1	1–2:1	1:1, 1–2:1
Abaxial epidermis shape	polygonal	polygonal	polygonal	polygonal	polygonal to interlocking (same as adaxial epidermis)

TABLE 2. *Continued.*

	Macarisieae	Hypogyneae	Gynotrocheae	Rhizophoreae	Anisophylleaceae
Relative size	same or smaller than adaxial	same or usually smaller than adaxial	same or smaller than adaxial	same as adaxial	same or smaller than adaxial
Stomate type	brachyparacytic, anisocytic, few diacytic, anomocytic	brachyparacytic, anomocytic, paracytic (few diacytic, anisocytic)	brachyparacytic, few anomocytic, anisocytic	obscure but probably all cyclocytic with 5–10 subsidiary cells	brachyparacytic, anisocytic, diacytic, paracytic, anomocytic
Position	abaxial	abaxial	abaxial	abaxial	abaxial
Sclereids	absent	absent	absent	astrosclereids in 3 of 4 genera	absent
Trichomes	absent to very common simple; near veins or random	absent to occasional, simple, long; near veins and lamina	absent	absent	absent to occasional, simple, short to long
Hypoderm	occasional, 2 layered	occasional, 2 layered	absent	usually present, 2 layered	absent

features mentioned above. Juncosa (1984b) found that *Rhizophora* has the most specialized shoot apical morphology and hypocotylar anatomy, with *Bruguiera* more transitional to inland genera of Rhizophoraceae. Leaf samples of *Bruguiera* showed the lowest rank order and the highest number of free vein endings for the tribe, but they are not otherwise distinctive architecturally.

The principal morphological diagnostic features of the Anisophylleaceae are the alternate leaves and the absence of stipules. No microscopic features absolutely distinguish its four genera from the Rhizophoraceae. Features not shared by Rhizophoraceae are asymmetrical leaves, teeth and marginal glands almost entirely absent, acrodromous venation, highest vein order to ten, and free vein endings per areole to greater than 20. But within the Anisophylleaceae these features characterize fewer than all of the species of one genus. All remaining recorded features are also found within the range of the variable tribes of Rhizophoraceae and supply no basis for separating the Anisophylleaceae from the Rhizophoraceae. A good case can be made that the Rhizophoreae are the most distinctive group based on their various specializations, including cyclocytic stomata, unusual druse crystals, high-ranking brochidodromous venation, vivipary, and mangrove habit. Yet much other available evidence argues for the obvious relatedness of the 14 genera of Rhizophoraceae s. str. and for their general similarity to the Anisophylleaceae. The only "teeth" in the Anisophylleaceae, the shallow marginal glands in *Anisophyllea meniandii*, are too simple structurally to allow an opinion on their origin or homologies.

COMPARISONS WITH LEAVES OF OTHER FAMILIES

The leaf architecture of the Rhizophoraceae is sufficiently generalized that comparisons with this aspect of other families is usually not particularly useful in affirming relationships. However, several of the families mentioned below are distinctly unlike the Rhizophoraceae. Each of the families was chosen by Dahlgren (this volume) for closer scrutiny after extensive comparisons using a broad data base. We compared all of the available cleared specimens in the National Cleared Leaf Collection, singling out those genera and species in particular that had the most elaborate, character-rich architecture.

The most useful characters appear to be of complex genetic origin, including secondary architecture, leaf shape, marginal configuration (tooth shape, gland type, and orientation of the related venation). The marginal configuration of the Cunonioid/rosoid leaf, with the internal epithem and the strongly converging marginal veins producing a hydathodal tooth, appears complex and monophyletic. It appears nowhere else than in the rosoid alliance as understood in all of the major current phylogenetic systems. However, there is insufficient information on the Macarisioid tooth type. The apiculate, deciduous gland serviced by a usually small single vein seems widespread and is probably not monophyletic, at least as the structure is detected in clearings.

Celastraceae

The ovate or elliptic leaves of this family are brochidodromous or eucamptodromous and of generally low rank order; the margins are faintly toothed and structurally Macarisioid. *Elaeodendron aethiopicum* and *Celastrus pringlei* have a single dominant vein that arises from a secondary or tertiary loop. It ends just below an apicular gland that is oriented adjacent to or points toward a sinus. All associated minor veins are decurrent on the dominant veinlet and do not participate in vascularizing the gland. In *Celastrus racemosus*, the tooth shape is Macarisioid but no dominant vein approaches the substantial gland. Two or three smaller marginal veins approach the gland but not closely.

A number of leaf characters of this family, particularly the secondary and higher order vasculature and the tooth type, are quite compatible with the Rhizophoraceae.

Cunoniaceae

The leaves have prominent teeth with three converging veins leading to an internal epithem. The converging veins have perpendicular cross braces, giving the Cunonioid tooth a unique appearance but not hiding an obvious similarity to the slightly simpler rosoid tooth. This type of tooth was held by Hickey & Wolfe (1975) to be ancestral to the rosoid tooth, an idea compatible with modern ideas concerning relationships between Cunoniales and Rosales. There is no similarity to the Rhizophoraceae at all.

Cyrillaceae

The two specimens available here, representing *Purdiaea nipensis* and *Cyrilla nipensis*, have elliptic to obovate leaves with entire margins. The brochidodromous secondaries are straightened into a collector vein or are looped, respectively. While *Purdiaea* is unexceptional in its higher-order venation and other features, the *Cyrilla* specimen does have incomplete venation with 15–20 vein endings per undefined aerole. It has stellate hairs of a type not seen in the Rhizophoraceae. The absence of teeth makes it impossible to compare marginal features productively, but the trend toward development of a strong submarginal collector vein in *Purdiaea* is not noted in the Rhizophoraceae.

Elaeocarpaceae

Leaves of this family show broad variation in the level of specialization (rank order), ranging from the 1r1 brochidodromous arrangement of *Elaeocarpus arnhemicus* to the 4r leaves of the genus *Sloanea*. Margins are toothed in all specimens seen, and the secondary architecture ranges from brochidodromous to forked craspedodromous. None of the observed patterns of higher-order venation or areolation can negate relationships with the Rhizophoraceae, nor does the tooth type. The teeth are typically Macarisioid with the strong medial vein servicing a prominent apiculate gland that often points to the sinus. The decurrent branching veins attached to the median vein diverge, often in a falcate curve, and they show no tendency to be involved in tooth venation. This family shows the closest resemblance to Rhizophoraceae on the basis of the leaf architecture.

Erythroxylaceae

The leaves examined have a secondary architecture of looped brochidodromous veins with irregular higher-order domains with a few unique or specialized features. Their level of organization is low first rank. Since the margins are entire, no tooth data are available. In most *Erythroxylon* species examined there is a rounded projecting apical gland vascularized by the midrib. They look the most macarisioid-like in a species from Java. Most of the glandular tips do not resemble the marginal features in the Rhizophoraceae. The family has trends of secondary and tertiary architecture unlike the Rhizophoraceae, including helicoid and admedially dendritic fourth- and fifth-order veins (*E. obtusifolium* from Sri Lanka) and secondaries closely spaced with higher-order veins parallel within the intercostal areas (*E. urbanii* from Puerto Rico).

Flacourtiaceae

Leaves of this large family vary greatly in size, shape, and secondary-venation patterns. Among the toothed leaves, two patterns are found, neither resembling the Rhizophoraceae. One of these has a Cunonioid vascular pattern with a strong median bundle that merges with two strongly converging lateral veins just below an apiculate tooth. The three converging veins are perpendicularly cross-braced with three or four minor veins. The other tooth type has one strong medial vein ending at the tooth apex, which may or may not have once had an apicular gland. Only one branch on the distal side passes through the sinus margin, providing it with conspicuous vascularization. No flacourtiaceous leaves seemed to approach the Rhizophoraceae architecturally.

Geraniaceae

Leaves of this family are often toothed and broadly elliptic. A principal characteristic of the family is parallelodromous secondary venation. Higher-order venation is not distinctive, and the low rank order (2r1) reflects the paucity of distinctive comparative architectural characters. The teeth are typically rosoid throughout all samples examined and therefore quite different from the Rhizophoraceae. *Viviana crenata* (Vivianaceae or Geraniaceae) is typically geranioid, including the presence of the rosoid tooth.

Hugoniaceae

The four *Hugonia* leaf specimens examined are generally compatible with Rhizophoraceae. The secondary architecture is eucamptodromous or looped brochidodromous, and the rank order ranges from 2r to 4r. The crenate margins have teeth very similar to the Macarisioid type. The tooth is generally incurved with the deciduous glandular apiculum pointing toward or located in the sinus. A single large vein, apically curved, arises from the secondary arch or loop and ends below the apiculum. It is associated with branching loops and minor veins that recurve or otherwise show no tendency to converge on the tooth. No features negate relationship with the Rhizophoraceae.

Ixonanthaceae

The three genera (five species) sampled here generally resemble the Rhizophoraceae, although the secondary architecture includes semicraspedodromous as well as brochidodromous types. Teeth are not universal but are found in *Octhocosmus*, and in a reduced form in *Ixonanthes*. Best-developed toothed margins are crenate with the glandular apiculae so "distal" on the tooth as to be on the proximal side of the sinus. A prominent vein arises from a secondary loop, sometimes in an organized semicraspedodromous pattern, and ends just below the gland. Some of the minor veins branching from this trace tend to converge toward the pad below the gland. This represents a significant difference from the Macarisioid tooth. Convergence of several veins toward the gland is a major characteristic of the Cunonioid/Rosoid/Fuchsioid type, although it appears to be an independent trend in the Ixonanthaceae. Other distinctive trends in this family include development of an entire leaf with a fibrous marginal vein in *Klainedoxa* and in *Irvingia*, and semicraspedodromous venation in *Octhocosmus*.

Lepidobotryaceae

The materials examined here are ovate leaves with entire margins and eucamptodromous secondary architecture. Intercostal areas are irregular, as are most of the tertiary domains and areoles. Some percurrent tertiaries are present. These unspecialized examples, *Papania scandens* and *Sarcotheca ferruginea*, are generally compatible with the Rhizophoraceae.

Oxalidaceae

Oxalis acuminata and the other species examined are trifoliate with entire ovate leaflets, which may be ciliate, looped brochidodromous, and with percurrent or irregular tertiaries. The reduced number of vein orders, five or six, and generally reduced appearance are compatible with the Rhizophoraceae.

Linaceae

The samples representing seven species are all more specialized than any Rhizophoraceae described. The secondary architecture is brochidodromous or eucamptodromous, but this ends the similarities. Tertiary and quaternary venation is virtually parallel, being perpendicular to the axis of the intercostal areas (*Roucheria griffithiana*) or parallel to them (*Roucheria calophylla*). *Linum* shows tendencies toward acrodromy and has fine, papillate/serrate, unicellular teeth. No multicellular teeth are present. Tooth glands in *Roucheria* are somewhat Macarisioid in appearance, as a median vein arises from a submarginal loop, ending just below the gland. However, there is also a definite tendency for lateral veins to converge toward the gland, a condition not seen in Rhizophoraceae. In *Linum* and *Reinwartia*, the small marginal projections are multicellular but not glandular or vascularized. It seems doubtful that the Rhizophoraceae leaf type has any close relationship with leaves of this family.

Rosaceae

This family is quite variable, and several types of secondary venation and teeth are found that bear much closer examination. *Fragaria* species generally have rosoid teeth, as does *Holodiscus discolor*, although the latter's medial vein is dominant, with the lateral ones being nearly absent. The marginal teeth of *Cotoneaster pyricantha* and *Kageneckia lanceolata* have deciduous apiculae and prominent medial tooth veins. Convergent lateral veins are present at most teeth or may not be obvious. The incurved appearance of the *Cotoneaster* tooth form is remarkably similar to the Macarisioid tooth.

Saxifragaceae

All leaves examined show a typical Rosoid hydathodal tooth with converging marginal veins that end in a flaring submarginal vascular plexus. They show no relationship to structures of the Rhizophoraceae.

Zygophyllaceae

The ovate leaves of this family are generally not toothed, and they have brochidodromous venation with a different appearance of areolation than Rhizophoraceae. One specimen, representing *Guaiacum sanctum* L., is craspedodromous with two or three small pointed teeth. A tooth is vascularized by a craspedodromous secondary vein that ends below its tip. There is apparently no apiculum or epithem at the tooth. Some minor veins form a converging buttress on the tooth vein. Overall, the tooth does not resemble Macarisioid architecture nor do the leaves resemble those of Rhizophoraceae in other respects.

WOOD ANATOMY

In the comparative wood anatomical literature, only two studies were found that were based on a comprehensive generic sample, those by Marco (1935) and by van Vliet (1976).

It should be noted that neither author developed a major operating hypothesis that the genera of Anisophylleae should be segregated as a separate family nor did their data and analyses support that view. Among the wood features they listed, only those mentioned below may have value in distinguishing the families. Table 3 provides a list of features we believe to have promise in differentiating the tribes and families.

Vessel tangential diameters of Anisophylleaceae overlap the high end of the range of Rhizophoraceae values, but they have the highest average and absolute values for this feature. Average vessel element length of the two families overlaps entirely, but Anisophylleaceae are at the short end of the range. Pores per square millimeter are the lowest for Anisophylleaceae with almost no overlap in the ranges for Rhizophoraceae. This correlates well with the high vessel tangential diameters. A computation of relative parabolic flow rates per mm^2 (Zimmermann, 1983) shows equivalent ranges with the Anisophylleaceae producing their flow rates with fewer pores and larger diameters on the average. The calculations were made using pooled data from the literature and are only indicative.

Macarisieae and Gynotrocheae have simple and scalariform perforations, while these in the Rhizophoreae are exclusively scalariform. Rhizophoreae also have the shortest vessel element lengths for the family, a character normally correlated with simple perforations (Dickison, 1975). It may be that efficiency of conduction (high flow rates) is not selected for in the mangroves. The generally small statures, coriaceous leaves, and restriction to saltwater habitats suggest the need to conserve water rather than to maximize its flow.

No other features—including fiber-tracheids, parenchyma or rays—seem to provide distinctive or mutually exclusive characters for the two families. Many of the characters are quite diagnostic for the genera, but differentiation of the tribes and of the two families is less readily accomplished. This is mostly due to very wide variation among the genera of Rhizophoraceae. The obvious distinctiveness of the Rhizophoreae is paralleled by the leaf data and can no doubt be explained by habitat specialization.

In other characters studied, the Anisophylleaceae show no similarity to the Rhizophoraceae. Chenery (1948) and Kukachka & Miller (1980) noted a positive aluminum test for the family, which is not shared by the Rhizophoraceae. Behnke (1981, 1984) noted S-type sieve element plastids in Anisophylleaceae and Myrtales but P-type in the Rhizophoraceae. In their embryological paper, Tobe & Raven (1987a) pointed out strong similarities of the Anisophylleaceae to the Myrtales and distinct differences with the Rhizophoraceae. However, they (1987b) later concluded that Anisophylleaceae and Rhizophoraceae do share enough developmental homologies to hypothesize common ancestry. The

TABLE 3. *Summary of selected wood features of the Anisophylleaceae and tribes of Rhizophoraceae.*

Character	Macarisieae; Hypogyneae	Gynotrocheae	Rhizophoreae	Anisophylleaceae
Vessel frequency (mm^2)	4–41 (138)	3–29	6–68	1–12
Vessel tangential diameter (μm)	21–340	71–300	34–130	84–430
Vessel element length (μm)	520–2,340	420–1,790	220–1,660	220–1,320
Perforations	simple/scalariform	simple/scalariform	scalariform	simple
IV pitting	alternate, opposite, transitional	alternate, opposite, transitional, scalariform	scalariform, transitional	alternate, with frequent coalescent apertures
Vessel-ray pitting	opposite, transitional, scalariform circular to elongate	alternate, opposite, reticulate circular to elongate	opposite to reticulate half-bordered to simple	rare, alternate to reticulate round to elongate
Fiber-tracheid length (μm)	960–3,390	1,210–3,480	libriform only 710–2,400	840–3,220
Ray type, seriation	heterocellular I, II; 1–5 seriate	heterocellular II, 2 distinct sizes; 1–32 seriate	heterocellular II, III, occasionally homocellular; 1–7 seriate	heterocellular II, 2 distinct sizes; 1–20 seriate
Ray tails, sheaths	1–36 square or erect cells	no tails, occasionally sheath cells	infrequent sheath cells	broad multiseriate, occasional sheath cells
Crystals	ray/axial parenchyma solitary, frequent or infrequent	ray/axial parenchyma solitary or clustered, frequent	ray parenchyma solitary	ray/axial parenchyma solitary, usually chambered to absent

perspective of vegetative anatomy alone is insufficient at present to resolve substantially this problem.

On the basis of their lack of vestured pits and intraxylary phloem and because of their possession of the Macarisioid tooth, the Rhizophoraceae s. str. appear to have no relationship to the Myrtales. Leaf teeth as known in all of the Rosales and Myrtales thus far examined are "rosoid," symmetrically vascularized by two to several converging veins surmounted by a secretory epithem, a submarginal foramen, and a connection to the surface through stomatelike pores. The tooth sinus is never reported to be included in the tooth vascularization. As described earlier here, the Macarisioid tooth is different in all respects. Thus far, the closest similarities to the Macarisioid tooth structure, and the general leaf architecture, can be found in the Dilleniid line. The Celastraceae (Celastrales), Elaeocarpaceae (Malvales), and Cyrillaceae (Ericales or Theales) are commonly classified in that lineage. Similarities seem more distant with the Hugoniaceae (Linales of Cronquist), Lepidobotryaceae (Geraniales of Dahlgren), and Oxalidaceae (Geraniales).

Considering that the field of comparative wood anatomy has a long established tradition, the results of comparisons among the families mentioned in this study are uncomfortably ambiguous. The newer field of leaf architecture has an equally well-drawn glossary and some organized preliminary synthesis regarding the character syndromes and their evolution. Here, too, we are left with equally large ambiguities. While the treatments of leaf architecture of families are far fewer than those based on comparative wood anatomy, existing comprehensive collections of cleared leaves should at least partially compensate. Some of these ambiguities may vanish in the future when the developmental bases of architectural forms becomes better understood and when the homologies of features of some of the larger phylads have been studied.

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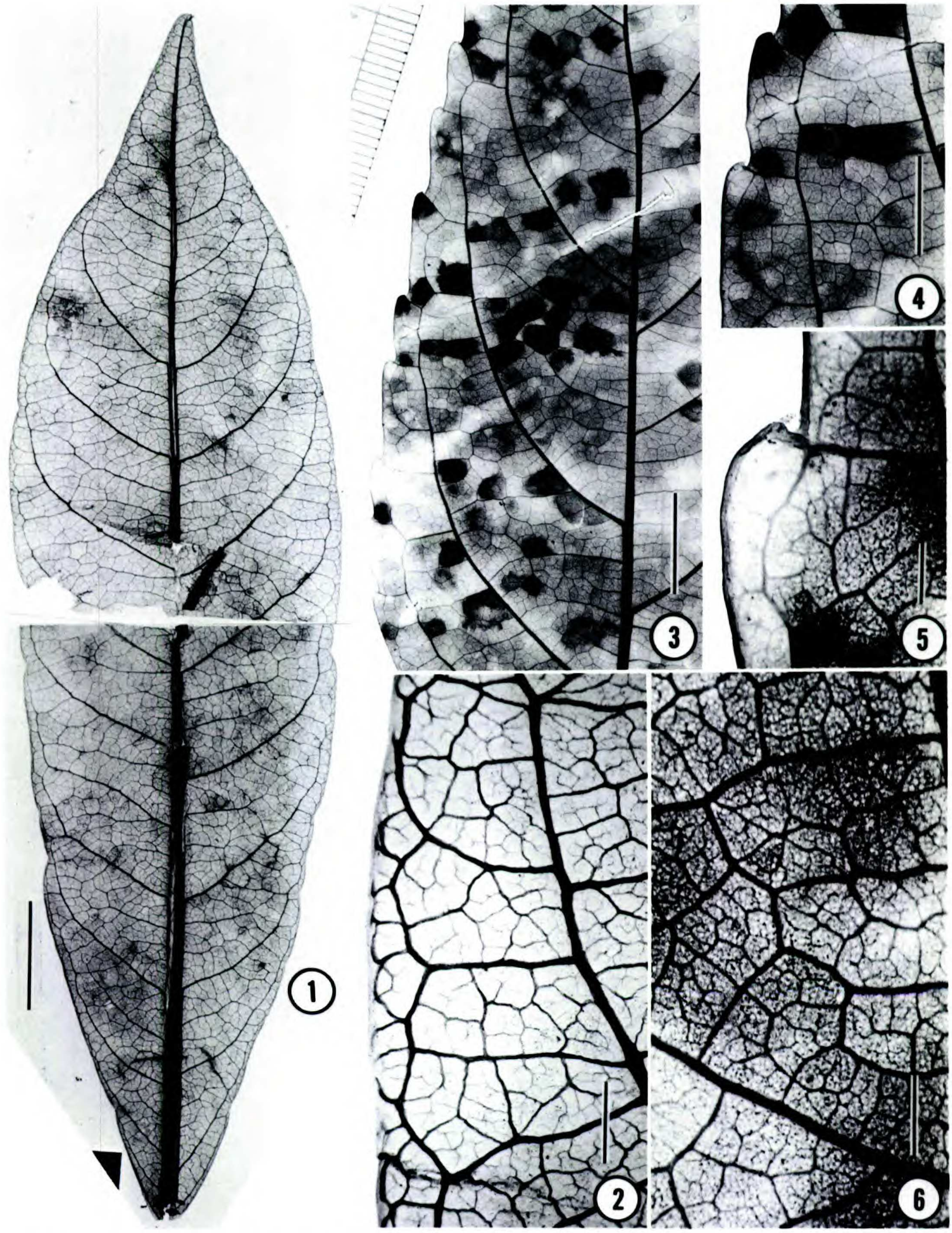
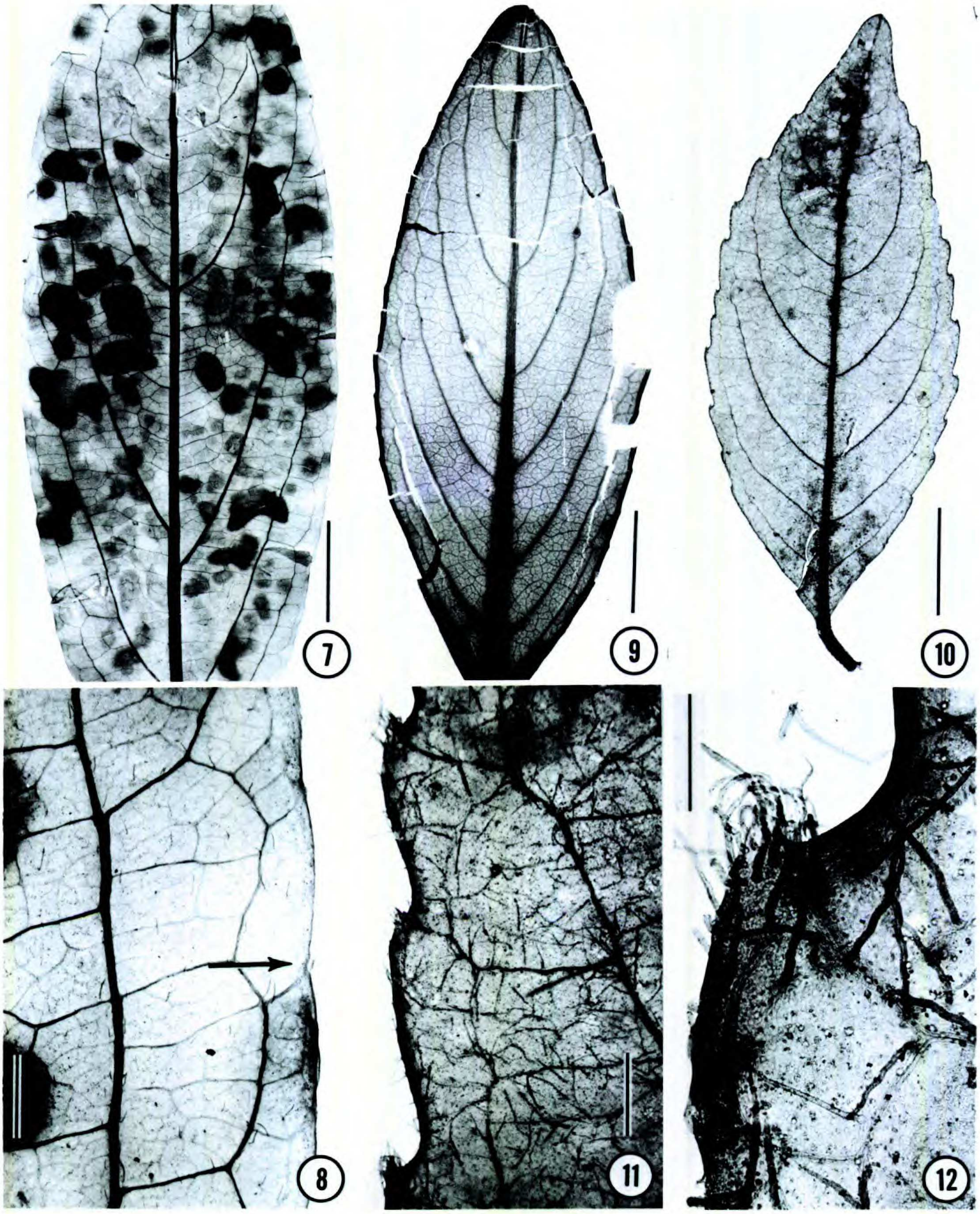
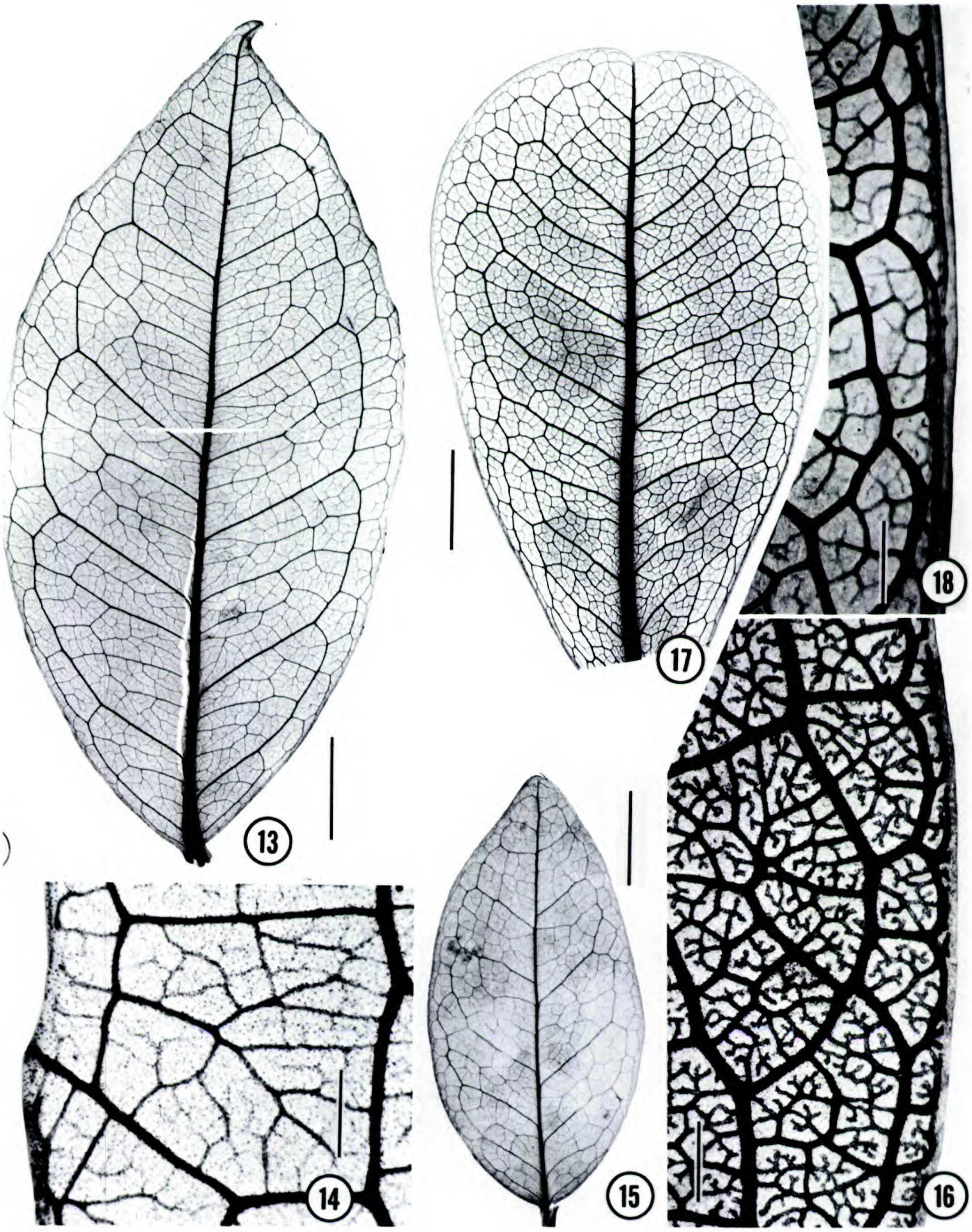


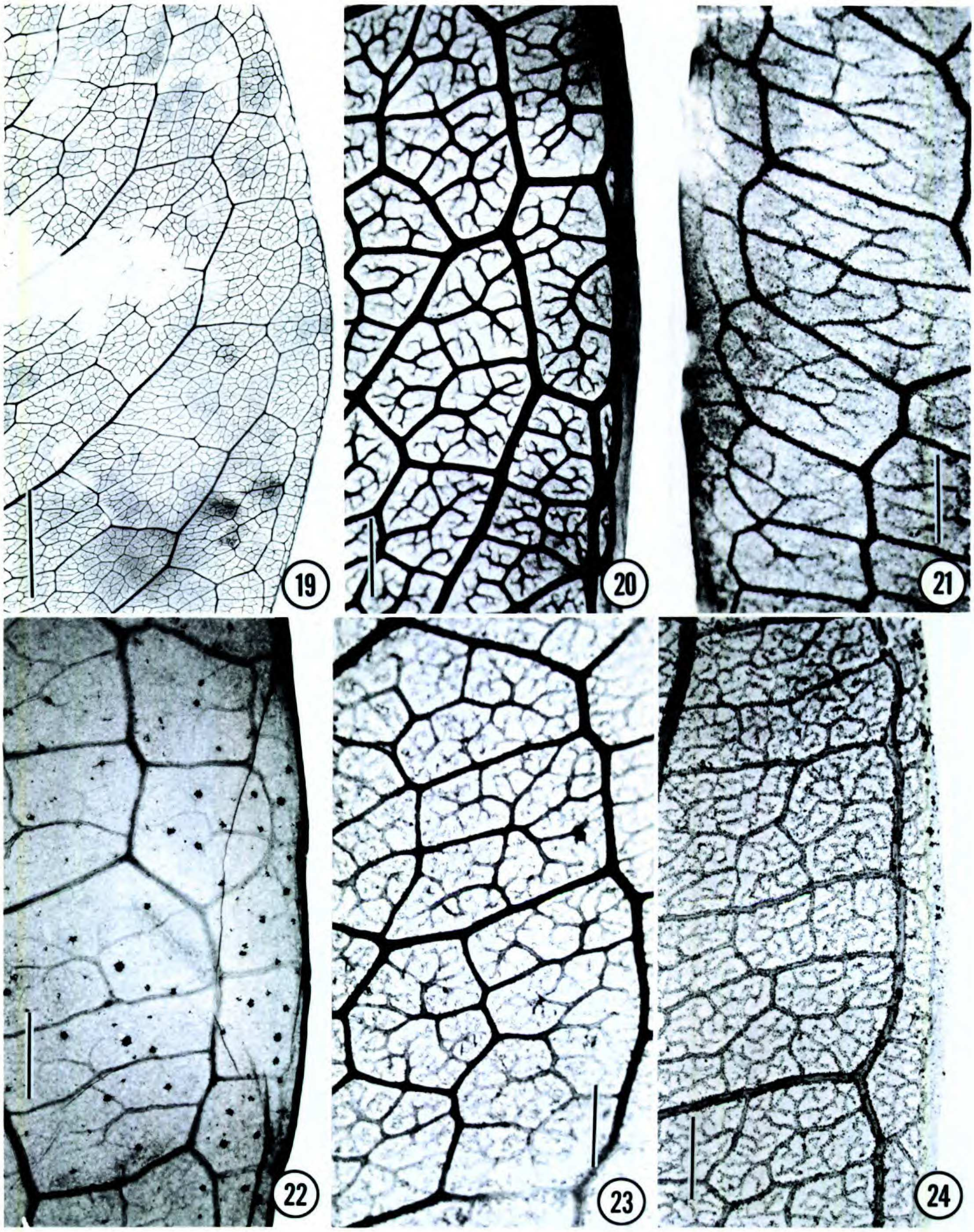
FIGURES 1–6. *Cleared leaves of Rhizophoraceae.—1.* Anopyxis calaensis, *showing eucamptodromous venation and entire, irregular margin.—2.* A. calaensis, *showing marginal venation and irregular higher-order domains.—3.* Blepharistemma corymbosum, *ovate leaf with toothed margin and eucamptodromous venation.—4.* B. corymbosum, *leaf margin showing the tooth veins arising from eucamptodromous loops.—5. Closeup of tooth in Figure 4 showing the vein bordering the sinus and ending below the apiculate gland.—6. Median portion of lamina of* B. corymbosum *demonstrating irregular polygonal tertiary and quarternary domains. Scale lines: Figures 1, 3 = 1 cm; Figures 2, 5, 6 = 1 mm; Figure 4 = 5 mm.*



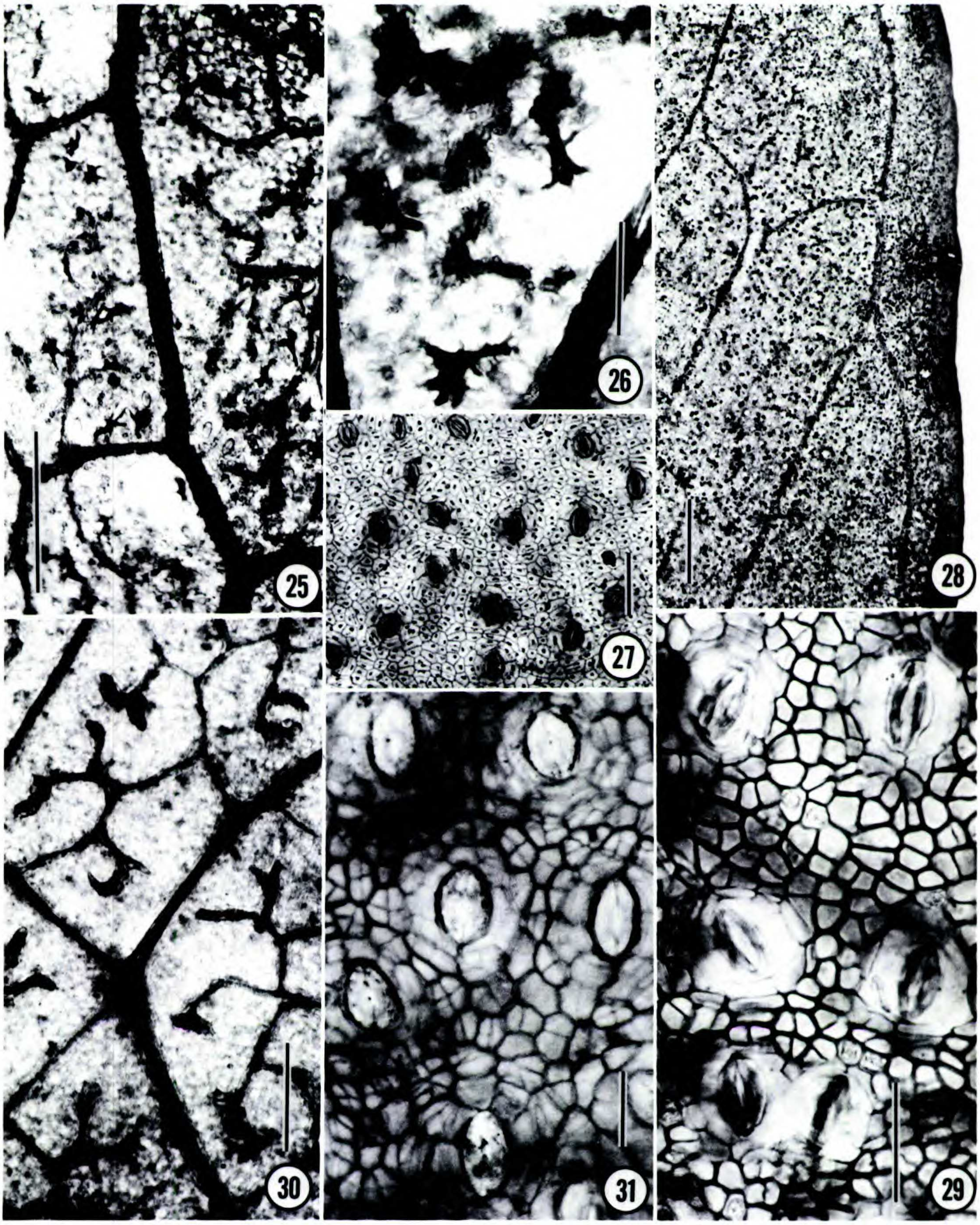
FIGURES 7–12. *Cleared leaves of Rhizophoraceae.—7.* Comiphyton gabonensis, *with strongly ascending eucamptodromous secondaries and irregular intercostal areas.—8.* C. gabonensis, *margin with reduced "tooth" with apiculate gland (arrow).—9.* Macarisia lanceolata, *with reduced teeth.—10.* M. pyramidata, *eucamptodromous leaf with well-developed teeth.—11.* M. pyramidata, *margin showing single tooth veins arising from the secondary loops.—12.* M. pyramidata, *showing vein entering a ciliate tooth from a symmetrical angle. Scale lines: Figures 7, 10 = 1 cm; Figures 8, 11 = 1 mm; Figure 9 = 5 mm; Figure 12 = 500 μm.*



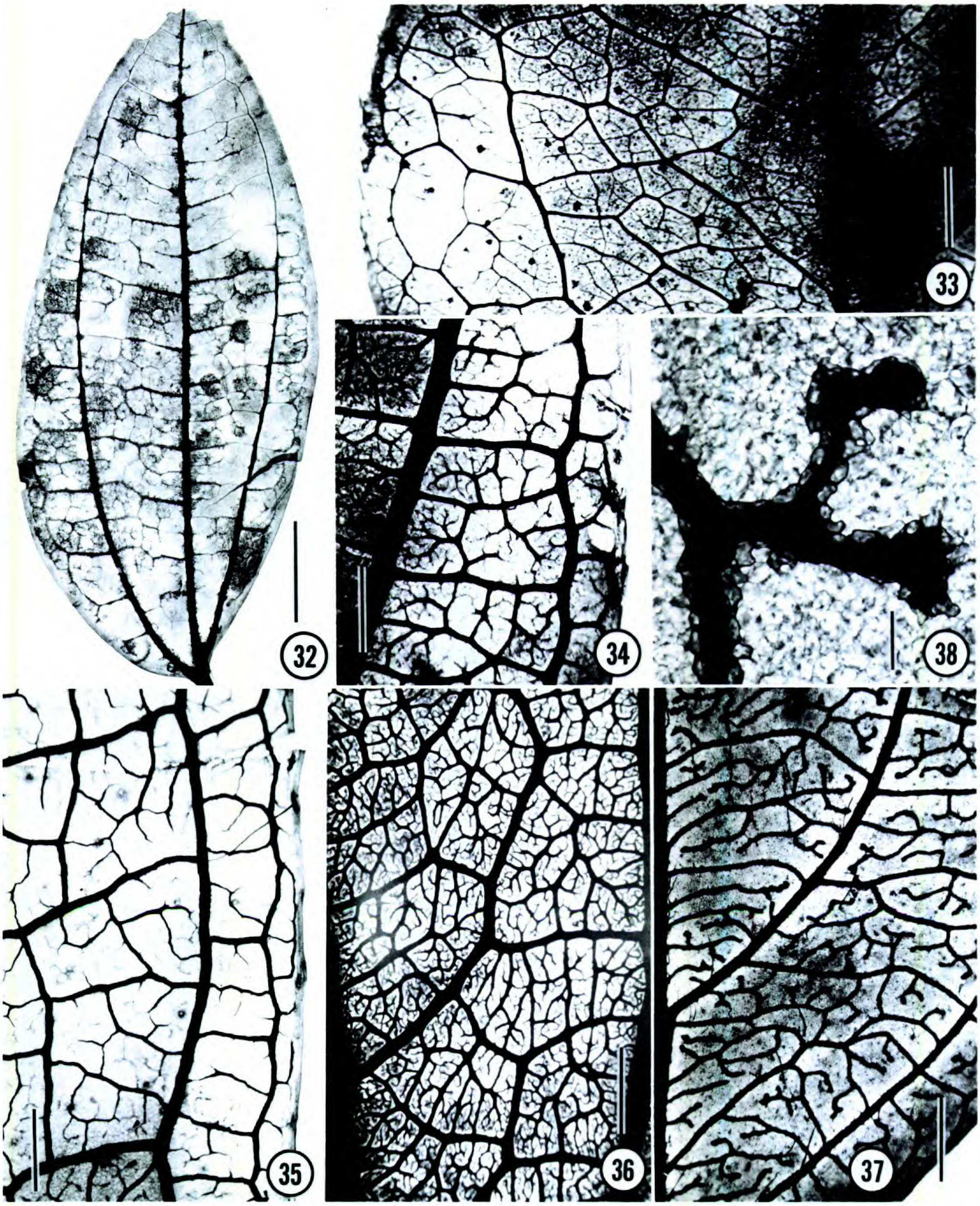
FIGURES 13–18. *Cleared leaves of Rhizophoraceae.—13.* Cassipourea guianensis, *showing looped brochidodromous venation with wide, regular intercostal areas and well-formed intersecondaries.—14.* C. guianensis, *showing single vein leading to small marginal tooth. Note that no other veins converge or participate in vascularizing the tooth.—15.* C. ceylanica, *showing the least organized intercostal areas among any of the cassipoureas examined. The margin is entire.—16.* C. ceylanica, *entire margin, irregular higher-order domains, and imperfect areolation with a highly variable number of free vein endings.—17.* Sterigmapetalum guianense, *showing looped brochidodromous venation and narrow intercostal areas.—18.* S. guianense, *showing the entire margin with looped venation. Scale lines: Figures 13, 15, 17 = 1 cm; Figures 14, 16, 18 = 1 mm.*



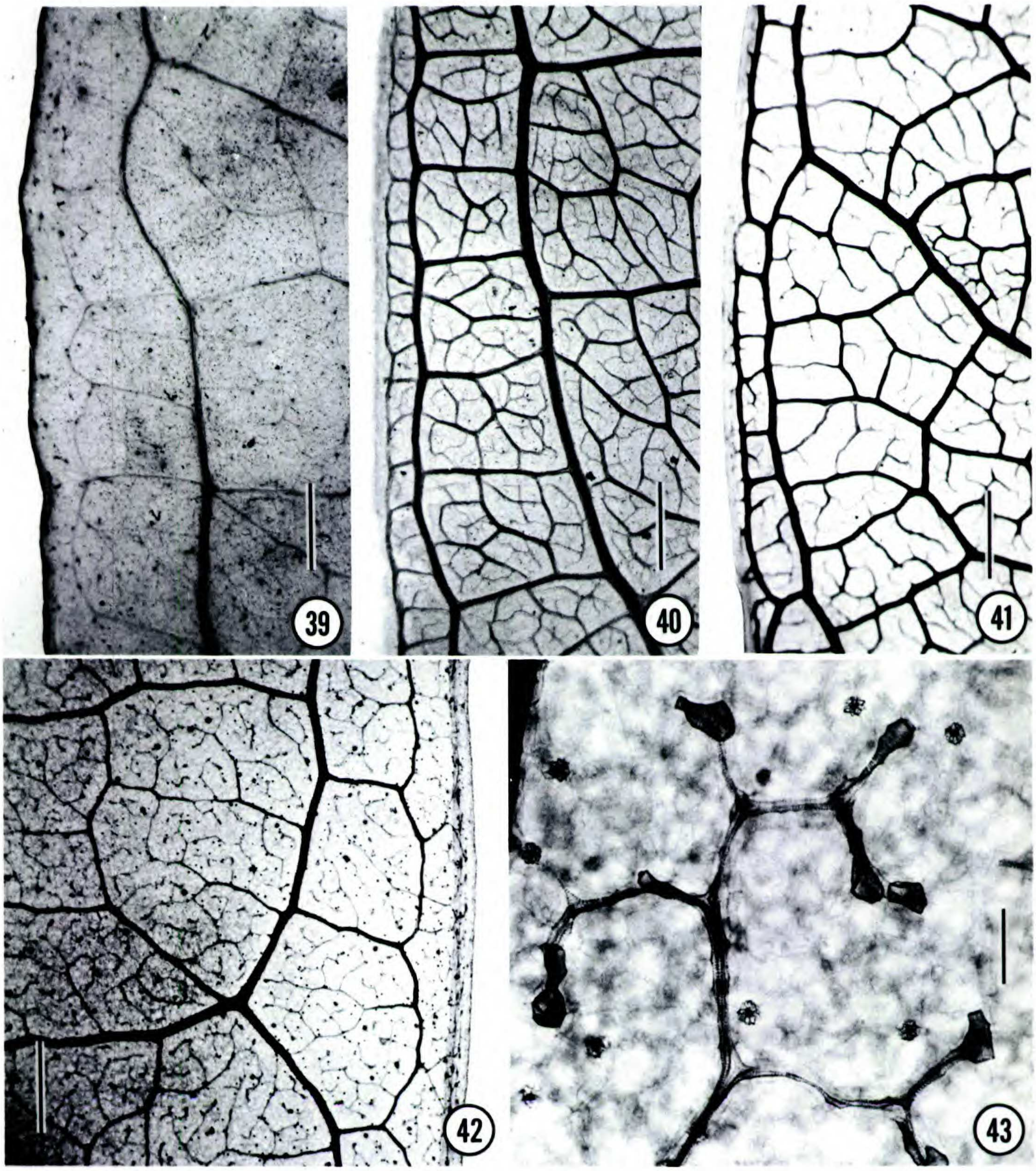
FIGURES 19–24. *Cleared leaves of Rhizophoraceae.—19.* Cassipourea barteri, *showing brochidodromous venation.—20.* C. barteri, *showing entire margin and imperfect areolation.—21.* Carallia brachiata, *with looped and elongated submarginal venation.—22.* Pellacalyx frustulata, *with an entire margin and looped submarginal venation.—23.* Crossostylis multiflora, *showing irregular quaternary domains and imperfect areolation.—24.* Gynotroches axillaris, *with eucamptodromous venation and regular percurrent quaternaries. Scale lines: Figure 19 = 1 cm; Figures 20–24 = 1 mm.*



FIGURES 25–31. *Cleared leaves of Rhizophoraceae.—25.* Rhizophora mangle, *showing obscure areolation.—26.* R. mangle, *showing astrosclereids in the mesophyll.—27.* Bruguiera gymnorrhiza, *showing cyclocytic stomata.—28.* Ceriops boiviniana, *leaf margin showing parallel secondaries and tendency toward development of a collector vein.—29.* C. boiviniana, *showing cyclocytic stomata.—30.* Kandelia candel, *areoles showing veinlets with tracheoidal endings.—31.* K. candel, *cyclocytic stomata. Scale lines: Figure 28 = 1 mm; Figures 27, 29, 31 = 100 µm; Figure 26 = 250 µm; Figures 25, 30 = 500 µm.*



FIGURES 32–38. *Cleared leaves of Anisophylleaceae.—32.* Anisophyllea cinnamomea, *leaf with asymmetrical base and basal acrodromous venation.—33.* A. griffithii, *leaf with brochidodromous looped margin and irregular higher-order venation.—34.* A. boehmii, *showing margin of eucamptodromous leaf.—35.* A. meniandii, *leaf with eucamptodromous entire margin.—36.* A. poggei, *mesophyll showing irregular higher-order venation.—37.* A. disticha, *mesophyll showing large, incomplete areolation.—38.* A. disticha, *veinlets showing differentiated sheath cells. Scale lines: Figure 32 = 1 cm; Figures 33–37 = 1 mm; Figure 38 = 100 μm.*



FIGURES 39–43. *Cleared leaves of Anisophylleaceae.—39.* Anisophyllea pomifera, *showing looped margin.—40.* Combretocarpus rotundatus, *margin of eucamptodromous leaf.—41.* Polygonanthus amazonicus, *margin with brochidodromous secondaries and imperfect areolation.—42.* Poga oleosa, *margin with brochidodromous secondaries and imperfect areolation.—43.* P. oleosa, *tracheoidal vein endings and druses. Scale lines: Figures 39–42 = 1 mm; Figure 43 = 100 µm.*